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On the affinities of the Filicineæ.

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No department of botany is more fascinating than the study of the phylogeny of the different groups of plants and their mutual relationships. The pteridophytes have naturally attracted special attention from their acknowledged affinity on the one hand to the bryophytes, and on the other to the flowering plants; but notwithstanding the numerous investigations upon them, there is still much difference of opinion respecting affinities among themselves and to the neighboring groups.

The present paper was prompted by a recent very suggestive and interesting article by Bower,[1] in which he maintains, with a good show of reason, the hypothesis most generally accepted at present as to the origin and affinities of the Filicineæ, viz.: the primitive character of the Hymenophyllaceæ and the derivative nature of the other Filicineæ. He shows by a careful comparative study of the meristems of the different members of the sporophyte that there is a regular increase in complexity from the Hymenophyllaceæ to the Marattiaceæ, and as he thinks to the Ophioglosseæ, though admitting certain difficulties in the latter case.

Having devoted much time to the study of these problems myself, and having reached somewhat different conclusions, this paper is presented to call attention to certain phases of the above view which it is believed are not warranted by facts.

According to this view the leptosporangiate ferns are regarded as the most primitive of the Filicineæ, and, of these, the Hymenophyllaceæ, undoubtedly the simplest in structure, also the most primitive, and probably derived from some form intermediate in character between existing bryophytes and the higher green algæ. These conclusions are based upon the very simple protonema-like prothallium of some species of Hymenophyllum, which it is assumed resembles the ancestral form from which bryophytes and pteridophytes both sprung. Grave difficulties, however, arise as

[1] The comparative examination of the meristems of ferns, as a phylogenetic study Ann. of Bot. iii, no. 11.

soon as we attempt to homologize the sporophyte of any leptosporangiate fern with that of any known alga or bryophyte. Anything in the least resembling the epidermal sporangia of the Filices is absolutely unknown outside of the group, and the high degree of development of the body of even the simplest of these is separated by an immense distance from the sporangium of any known form among either bryophytes or algæ. It must be borne in mind that the prothallium of a Hymenophyllum corresponds not merely to the protonema of a moss, but to the protonema *plus* the leafy sexual plant.

If we go back to the older botanists we find a different view as to the origin of the pteridophytes, though here also the leptosporangiate ferns seem to be regarded as the more primitive forms. According to this earlier view the pteridophytes probably originated from some simple form allied to the Hepaticæ. The evident resemblance between such a form as Anthoceros, for example, and an ordinary fern-prothallium is obvious, and I hope to show that there is some good reason for reconsidering, at least, this older view.

Leitgeb[2] calls attention to the well-known but significant fact that among the Anthoceroteæ alone, of all known bryophytes, the growth of the sporogonium is unlimited, continuing to grow at the base as long as the plant lives. The sporogonium is relatively very large and contains abundant green parenchyma with large intercellular spaces communicating with stomata of the same structure as those of the higher vascular plants, so that so far as assimilation is concerned, it is quite independent of the oöphyte. Add to this that the columella, both in structure and position, closely resembles the young axial fibro-vascular bundles of the embryos of pteridophytes, and we see how closely the sporogonium of Anthoceros approaches to what might be called an independent vascular plant. If we could imagine such a sporogonium to develop a root fastening it in the ground, and thus rendering it entirely independent of the oöphyte, we should have the simplest possible form of a pteridophyte.

In Anthoceros, however (and the same is true throughout the bryophytes), the spores are of strictly endogenous origin, *i. e.*, the plant is eusporangiate, and this, as I shall endeavor to show, is probably the primitive condition among the Filicineæ.

Because the higher pteridophytes and spermaphytes are eusporangiate is no reason why this should not be the primi-

[2]Untersuchungen über die Lebermoose.

tive condition. It would be as reasonable to argue that, because in man the hand is pentadactyl, while in the horse it is monodactyl, that the latter approaches in this respect more nearly the primitive mammalian type than does the former, being admittedly an animal of lower rank than man.

The Leptosporangiatæ may therefore be looked upon as bearing much the same sort of relation to the eusporangiate pteridophytes and spermaphytes as some such peculiarly specialized group as the ungulates bears to the other mammalia.

If we examine the different groups of the pteridophytes, where shall we find the form that corresponds most nearly to this assumed primitive type? I think the answer is Ophioglossum. In such a form as O. vulgatum the sporophyte is reduced to almost its simplest expression, little more than a single two-lobed leaf and a few roots of the simplest form, the stem being reduced to a minimum. The sporangia are mere cavities in the tissue of the fertile leaf-segment, scarcely indicated on the surface and covered over with an undifferentiated stoma-bearing epidermis. If we compare this with the sporogonium of Anthoceros we shall find in the latter that the greatest difference, aside from the absence of true fibro-vascular bundles, is that the sporogenous tissue forms a continuous layer surrounding the columella. The epidermis develops stomata of precisely the same character as those of Ophioglossum and other vascular plants. Separate the sporogenous tissue in distinct sporangia, each with its own external opening, and develop a few vessels in the columella, and we have a structure approaching very near to what really attains in the fertile segment of the leaf of Ophioglossum.

The tissues of the Ophioglossaceæ are remarkably simple in structure, this being most noticeable in Ophioglossum.[3] In the latter the predominating tissue is an undifferentiated spongy parenchyma.[4] No special hypoderma is recognizable, the absence of the abundant sclerenchyma of most pteridophytes being very noticeable, as well as the small size and simple structure of the fibro-vascular bundles. The stem and root grow from a single apical cell, indicating thus, according to Bower's view,[5] a primitive condition as compared with the higher pteridophytes and spermaphytes.

Unfortunately our knowledge of the prothallium and em-

[3] Gœbel, "Outlines," p. 250; De Bary, "Comparative Anatomy," etc.

[4] Op. cit.

[5] L. c. p. 318, 366.

bryo is so scanty as to make it impossible to draw positive conclusions from a comparison with Anthoceros. It is, however, highly probable that the prothallium is more like that of the Marattiaceæ than any of the other pteridophytes, as the sporophytes of the two agree in many particulars, and this harmonizes with our very imperfect knowledge of the prothallium derived from the works of Hofmeister[6] and Mettenius.[7] The prothallia of the Marattiaceæ[8] show most surprising analogies with the liverworts, and, in some noticeable particulars, with Anthoceros. The archegonia are deeply sunk in the oöphyte, as in Anthoceros, and, according to Jenkman,[9] possess three canal cells, in which respect, so far as at present known, they stand alone among the ferns, but approach the bryophytes. The antheridium, also sunk in the prothallium, recalls, though distinctly, the endogenous antheridium of Anthoceroteæ, the only ones of all known bryophytes in which this is the case.

The statements of Hofmeister[10] and Mettenius,[11] that the prothallia of the Ophioglosseæ are destitute of chlorophyll, require confirmation; and it is highly probable, as Gœbel suggests,[12] that the earlier stages, at least, are provided with chlorophyll. Until quite recently the same statement was universally accepted for Lycopodium, but the researches of Treub[13] and Gœbel[14] have shown that this is not the case, but that the prothallia of Lycopodium are abundantly provided with chlorophyll.

What relation, then, do the Ophioglosseæ bear to the other Filicineæ? As Bower has shown,[15] there is a complete series of homosporous Filicineæ, with the Hymenophyllaceæ at one end and the Marattiaceæ, and perhaps the Ophioglosseæ, at the other; and this arrangement probably is the correct one.

Within the Ophioglosseæ the different species of Botrychium show a very beautiful series of forms connecting Ophioglossum with the Leptosporangiatæ. In the form of the sporangia, as well as in their position, Osmunda comes

6 Hofmeister, "Higher Cryptogamia," p. 307.
7 Gœbel's "Outlines," p. 245–46.
8 Jenkman, "Generation sexuél des Marattiacées."
9 Op. c. figs. 102, 103.
10 Loc. cit.
11 Loc. cit.
12 Loc. cit. p. 245.
13 Annals of the Bot. Garden of Buitenzorg.
14 Bot. Zeitung, 1887.
15 Loc. cit.

nearer to Botrychium than do the Marattiaceæ, although in some other respects this is not the case. While the fibro-vascular bundles of Ophioglossum are collateral[16] (which is also true of Osmunda[17]) those of Botrychium are concentric, this being particularly noticeable in the larger species, such as B. ternatum and B. Virginianum. In these larger species, too, there is some slight trace of a hypoderma distinct from the rest of the ground tissue, and the bundle-sheath is pretty well defined.

As has been shown, too, while in B. simplex the leaf is folded straight in the bud, in B. Virginianum it is bent over, thus approaching the circinate vernation of the Marattiaceæ and Filices.

If we assume Ophioglossum to be the higher form (being most strongly eusporangiate), it is certainly difficult to account for the gradual simplification of the tissues as we pass from the Filices through Botrychium or the Marattiaceæ. Such a simplification can not be accounted for from the habits of the plant, as it is neither an aquatic nor a parasite.

The greatest difficulty, however, it seems to me, in regarding the Hymenophyllaceæ as primitive forms as compared with the Marattiaceæ and Ophioglosseæ is the increase in the size of the prothallium as we go from the former to the latter. Bower[18] tries to explain this by assuming that the size and complexity of the prothallium are correlated with the increasing complexity of the sporophyte, and like it due to the change from a semi-aquatic to a purely terrestrial habit.

There are two objections to this view: First, if we admit that the cycads are related to the Marattiaceæ (which Bower seems to think very probable), we must suppose a reduction of the prothallium again to produce the heterosporous forms that must have intervened. That there should be an *increase* in the size of the prothallium up to a certain point, keeping pace with the development of the sporophyte, and then a retrogression, is difficult to understand, and is certainly improbable. If on the other hand we admit that the Marattiaceæ are primitive forms, allied, perhaps, to Ophioglossum, the massive character of the oöphyte is easily comprehensible, and the possible derivation of the cycads from them could then be understood by assuming a series ending in some heterosporous form leading up to the former.[19]

[16] De Bary, op. c. pp. 321, 364.

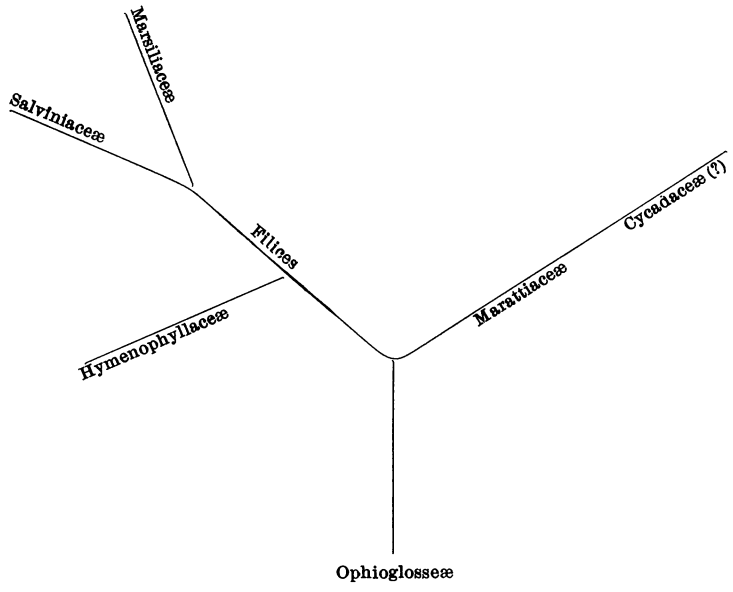
[17] De Bary, l. c.

[18] Op. cit., p. 370.

[19] Bower suggests that possibly Isoetes may be such a form, and this seems to be also the view of Vines.

The second difficulty mentioned is the fact that just those forms, viz., Ophioglossum and Equisetum, which are the most essentially eusporangiate of all pteridophytes, are characterized by the root and stem growing by a regular apical cell, a point that Bower regards as evidence of primitive structure.

The accompanying diagram will show the relationship assumed here:



It will be seen that there are two main branches, one through the Marattiaceæ, possibly terminating in the Cycadeæ; the other the Filices, giving rise to two branches ending in the two heterosporous groups, the Marsiliaceæ and the Salviniaceæ. The Hymenophyllaceæ, according to this view, must be looked upon as a degenerate group, the simple prothallium and sporophyte resulting from the semi-aquatic habit of the plants.

Just at what point the Leptosporangiatæ branched off, assuming the view here taken to be correct, it will be impossible to decide until the oöphyte of the different forms is better known than at present. The same difficulty is true

with regard to the origin of the Salviniaceæ, which are certainly not closely related to the Marsiliaceæ.[20]

With our very imperfect knowledge of the oöphyte of the Ophioglosseæ, it would be rash to assume that the group originated from the Anthoceroteæ; indeed there are very strong objections to be brought against such a view. In spite of the resemblance of the sexual organs of the Anthoceroteæ to those of the Marattiaceæ, they are nevertheless in their development much more like those of the other liverworts. Again, the Anthoceroteæ are peculiar in the single large chloroplast in each cell; recalling strongly, in this particular, such algæ as Coleochæte, where this is also the case, and suggesting a possible derivation from similar forms.

Nevertheless, since in Anthoceros there are such striking resemblances to the oöphyte of the Marattiaceæ, and the sporogonium becomes so nearly independent, we can readily conceive of some allied form with chloroplasts of the ordinary type, and with sexual organs approximating still more closely those of the pteridophytes, in which by the development of a root the sporogonium would become entirely independent. It would be but a step from such a form to the simpler Ophioglosseæ.

Bower[21] admits that some such view as the one advanced here is capable of defense, but does not believe it to be the true one. He does not, however, nor does any other botanist[22] so far as I know, give any satisfactory explanation of the origin of the sporophyte of Hymenophyllum from any known or even hypothetical ancestral form.

From the foregoing pages it is evident that there is something, at least, to be said in favor of assuming that Ophioglossum and the other eusporangiate ferns are primitive rather than derivative forms, but until the life-history of these forms, as well as of many of the Leptosporangiatæ is thoroughly known it will be unsafe to be too positive as to their systematic positions.

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[The author is anxious to procure material for the study of the development of the Ophioglosseæ and will be much indebted to any of the readers of the GAZETTE who can supply fresh fruiting specimens, especially of Ophioglossum. It is particularly desired to have fresh spores of as many species of the latter as possible.]

[20] See Campbell, "The systematic position of the Rhizocarpeæ," Bull. Torrey Bot. Club, October, 188-. Also, "Development of Pilularia globulifera," Ann. of Bot. vol. ii. no. 7.

[21] Op. cit. p. 374.

[22] I have not had an opportunity of examining Göbel's investigations on Hymenophyllaceæ in the Annals of the Botanical Garden of Buitenzorg.